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The importance of reforested and naturally regenerating young forest patches as secondary habitats for forest birds in the Biological Corridor La Gamba, Costa Rica

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Although the protection of tropical primary forests is of primary importance for conservation, secondary forests may help to reduce increasing forest fragmentation and related biodiversity loss. This study from the Pacific lowlands of Costa Rica evaluates the potential of secondary forests to provide additional habitat and to act as stepping stones for dispersal movements of forest species. Forest understory bird assemblages were assessed at five mature and five young forest sites using mist-netting. To identify important vegetation structures for forest birds utilizing disturbed habitats (including secondary forests), point counts were used to survey birds across a habitat gradient ranging from pastures to secondary forest of different successional stages. Furthermore, bird surveys were conducted at one reforestation site to document the colonization by forest birds over a short time span of five years after the implementation of the reforestation measures. Species composition differed significantly between mist-netting sites in mature and young secondary forest, nevertheless 66.1 % of the more abundant species could be recorded in both forest types. Richness of forest specialists assessed along the gradient of habitat disturbance increased significantly with increasing number of large trees, while other habitat variables were of no or only minor importance. At our studied reforestation site, species composition changed almost continuously with progressing forest succession over the period of five years, related to an increase of the relative richness of forest birds, while the total number of species per survey remained similar. Besides potentially representing important stepping stones for forest birds by facilitating crossings of open areas, our results indicate that secondary forest patches embedded with the human-modified landscape can represent important secondary habitats for a substantial proportion of forest birds. Considering the close relationship between the number of large trees and the richness of forest specialists, further research has to evaluate the potential of using fast-growing trees to more rapidly increase the conservation value of actively restored secondary forests for the recovery of forest birds.

Schulze C.H., Leidinger P., Paces B. & Reyes Páez A.F., 2019: Die Bedeutung von wiederbewaldeten und natürlich regenerierenden jungen Waldflächen als Sekundärhabitat für Waldvögel im Biologischen Korridor La Gamba, Costa Rica.

Obwohl der Schutz tropischer Primärwälder nach wie vor das naturschutzfachliche Hauptanliegen sein muss, können Sekundärwälder dazu beitragen, der zunehmenden Fragmentierung von Wäldern und den damit verbundenen Verlust an biologischer Vielfalt entgegenzuwirken. Diese Studie aus dem pazifischen Tiefland Costa Ricas untersuchte das Potenzial von Sekundärwäldern, als zusätzliche Lebensräume und als Trittsteine für die Ausbreitung von Waldarten zu fungieren. An jeweils fünf Standorten in weitgehend ungestörten Wäldern und jungen Sekundärwäldern wurden mittels Japannetzen Unterwuchsvögel erfasst. Um für Waldvögel wichtige Vegetationsstrukturen in gestörten Lebensräumen (einschließlich Sekundärwäldern) zu identifizieren, erfolgten Punktzählungen entlang eines Habitatgradienten von Weiden bis hin zu Sekundärwäldern verschiedener Sukzessionsstadien. Darüber hinaus wurden auf einer Wiederbewaldungsfläche Vogelerhebungen über einen kurzen Zeitraum von fünf Jahren durchgeführt, um die Besiedlung durch Waldvögel nach Umsetzung der Wiederbewaldungsmaßnahmen zu dokumentieren. Die Artenzusammensetzung unterschied sich deutlich zwischen den Netznetzstandorten in alten Wäldern und jungen Sekundärwäldern. Dennoch konnten 66,1 % der häufigeren Arten in beiden Waldtypen nachgewiesen werden. Der entlang des Habitatstörungsgradienten erfasste Artenreichtum an Waldvögeln nahm mit zunehmender Anzahl großer Bäume signifikant zu, während anderen Habitatvariablen keine oder eine nur geringe Bedeutung zukam. Auf der untersuchten Wiederbewaldungsfläche änderte sich die Artenzusammensetzung über den Zeitraum von fünf Jahren mit fortschreitender Sukzession mehr oder weniger kontinuierlich, einhergehend mit einer Zunahme des relativen Artenreichtums an Waldvögeln, wohingegen die Gesamtartenzahl pro Erhebung ähnlich blieb. Unsere Ergebnisse zeigen, dass die in der anthropogen stark veränderten Landschaft eingebetteten Sekundärwälder wichtige Sekundärlebensräume für einen erheblichen Teil der Waldvögel darstellen können. In Anbetracht des engen Zusammenhangs zwischen der Anzahl großer Bäume und dem Reichtum an Waldvogelarten sollte in weiteren Untersuchungen geprüft werden, inwieweit schnell wachsende Bäume den Wert von Wiederbewaldungsflächen für Waldvögel positiv beeinflussen können.

Keywords: secondary forest, reforestation, large trees, species composition, forest birds.

Introduction

Deforestation and land use have been identified as the main drivers for reducing the primary forest areas in the world's tropical regions (Turner 1996, Lamb 1998, Laurance 1999, Debinski & Holt 2000, FAO 2010). The resulting fragmentation of tropical forests negatively affects population dynamics of forest species and contributes to the ongoing biodiversity loss (Rosero-Bixby & Palloni 1998, Sala et al. 2000, Sodhi & Smith 2007, Harvey et al. 2008, Sodhi et al. 2008).

Remaining old-growth forests proved to be of prime importance especially for species with specific habitat dependencies, restricted geographical ranges and little or no tolerance to habitat fragmentation and landscape change (Stotz et al. 1996, Soh et al. 2006). This has been especially well documented for some tropical bird species (Kofron & Chapman 1995, Estrada et al. 1997, Fjeldså 1999, Blake & Loiselle 2001, Naidoo 2004, Waltert et al. 2004, Sodhi et al. 2005, Arriaga-Weiss et al. 2008, Sodhi et al. 2008, Maas et al. 2009). Although the conservation of tropical primary forests is still the main concern, due to their irreplaceable characteristics and high value for many tropical species (Dirzo & Raven 2003), secondary forests may help to reduce increasing forest fragmentation and related biodiversity loss (Chazdon et al. 2009, Seaman & Schulze 2010, Fahrig et al. 2011).

Nowadays, it is almost impossible to find pristine, undisturbed forests (Willis et al. 2004), and the small remaining forest areas are still in the focus of commercial or illegal logging activities (Bawa & Dayanandan 1997, Vitousek et al. 1997). Thus, in an attempt to compensate this loss, forest restoration and renaturation measures are implemented on degraded land (Lamb 1998, Rey Benayas 2000, Petit & Montagnini 2006). Despite efforts to mitigate the damage to nature, there are many limitations, especially of a monetary nature, which is why most forest regeneration takes place by passive restoration (natural regeneration) (Rey Benayas 2000), resulting in various types of secondary forests (Aide et al. 2000, Wright 2005, Guerrero & da Rocha 2010). Problems for natural regeneration can be a lack of a remaining seed bank or seed dispersal (Reid et al. 2008, Reid et al. 2012).

Regenerated secondary forests are classified as being suitable to support a certain fraction of biodiversity (Sodhi et al. 2004) with a positive species recovery over time (Grau et al. 2003, Dunn 2004). They maintain more forest-dependent species of higher conservation concern than extensive plantations (Peh et al. 2006, Edwards et al. 2010, 2011). Likewise, some studies suggested that forests with secondary growth are potential reservoirs of biodiversity (Chazdon 1998, 2008, Brook et al. 2006, Wright & Muller-Landau

2006a, 2006b, Barlow et al. 2007a, 2007b), and could also serve as temporal refuges, foraging areas and – most importantly – as landscape structures connecting remaining forest fragments (Myers 1997, Blake & Loiselle 2001, Chazdon 2003, Fischer et al. 2006, Höbinger et al. 2012). Therefore, even though they differ in structural and floristic composition from primary forests, they can contribute to the creation of biological corridors for forest species. Also, due to their relatively high productivity, these areas should be incorporated into agroecosystems, which consequently may benefit from indirect services (e.g. pollination and pest control) provided by forest species interacting with the surrounding human-dominated landscape matrix (Finegan 1992, Chazdon 2008).

Secondary forests are rapidly expanding in the tropics (Wright 2005). They are especially emerging in abandoned areas which are not further used for agricultural purposes (Thomlinson et al. 1996). Hence, they should be considered in approaches improving biodiversity conservation on a landscape scale.

In this study from the Pacific lowlands of Costa Rica, birds were used to study the capability of secondary forests to facilitate forest species at the margin of protected rainforest areas. We were particularly interested in the potential of these secondary forests to increase landscape permeability and to act as corridor habitats for forest birds. In particular, the following hypotheses were tested: (1) Although secondary forests can support a relatively high bird species richness, they are characterized by a distinct species composition. (2) Species richness and composition of forest species assemblages in disturbed habitats depend on larger trees representing a key habitat structure for forest species. (3) Species composition of secondary forests changes with progressing vegetation succession, (4) due to an increasing richness and abundance of forest-dependent species with progressing forest succession age. To test these hypotheses, we conducted mist-netting in order to compare understory bird assemblages of old-growth forests and young secondary forests created by reforestation measures. We further conducted bird surveys in a variety of habitats mimicking a forest succession sequence, and monitored changes of the bird assemblage of a young secondary forest over a time period of six years after reforestation measures were implemented.

Methods

Study area

The study area is located in the "Golfo Dulce" region of southwestern Costa Rica, between the "Piedras Blancas" National Park (including "Esquinas" Forest, Valley "Río Esquinas" and Valley "Río Bonito") and the "Fila Gamba". The Golfo Dulce region is classified as an important Endemic Bird Area (EBA 021: South Central American Pacific slope) hosting several range-restricted bird species (Stattersfield et al. 1998, Birdlife International 2012) and belonging to one of the most diverse regions in terms of faunistic and floristic richness within the tropical region of Central and South America (Hammel et al. 2004, Lobo Segura & Bolaños 2005). So far, more than 300 bird species (including several range-restricted species and subspecies of high conservation value) (Tebb 2008) have been recorded in our study area in the vicinity of the Tropical Research Station La Gamba (N 08°42.063′, W 083°12.102′).

The study area has an annual precipitation of 6,000 mm with a rainfall peak between August and November and lowest precipitation between January and March; the annual mean temperature is 28.5° C (Weissenhofer & Huber 2008). The natural vegetation is mainly represented by tropical lowland wet forest (Weissenhofer et al. 2008a). The surroundings of the village “La Gamba”, which is located in the center of our study area, are characterized by pastures with small and elongated forest patches, strips of gallery forests, few big plantations (e.g. oil palm), old (and mostly abandoned) agroforests (cacao) and annual cultures (e.g. rice) (Seaman & Schulze 2010, Höbinger et al. 2012).

Assessing understory bird assemblages in old-growth forest and secondary forest

To assess the understory bird assemblages of old-growth forest and young secondary forests, birds were mist-netted at five replicate sites in each forest type (Fig. 1). A one-way ANOSIM was used to test for differences in spatial distances between mist-netting sites belonging to the same habitat type. It did not indicate that sites belonging to the same habitat type were closer situated to each other than sites belonging to different forest types (Global $R = 0.002$, $p = 0.357$). Hence, we do not expect spatial autocorrelation to affect our analyses. At each site, six 12 m mist nests (2 with 16 mm mesh size, 2 with 30 mm mesh size, 2 with 45 mm mesh size) were used to trap birds during four mist-netting events. During each mist-netting event it was aimed to trap birds for a total of 15 hours, between 5:30–15:00 on the first day and between 5:30–11:00 on the second day. Hence, the total mist-netting effort per site should have been 60 hours. However, due to bad weather conditions (mist-nets were not operated during strong rain), the total mist-netting duration per site

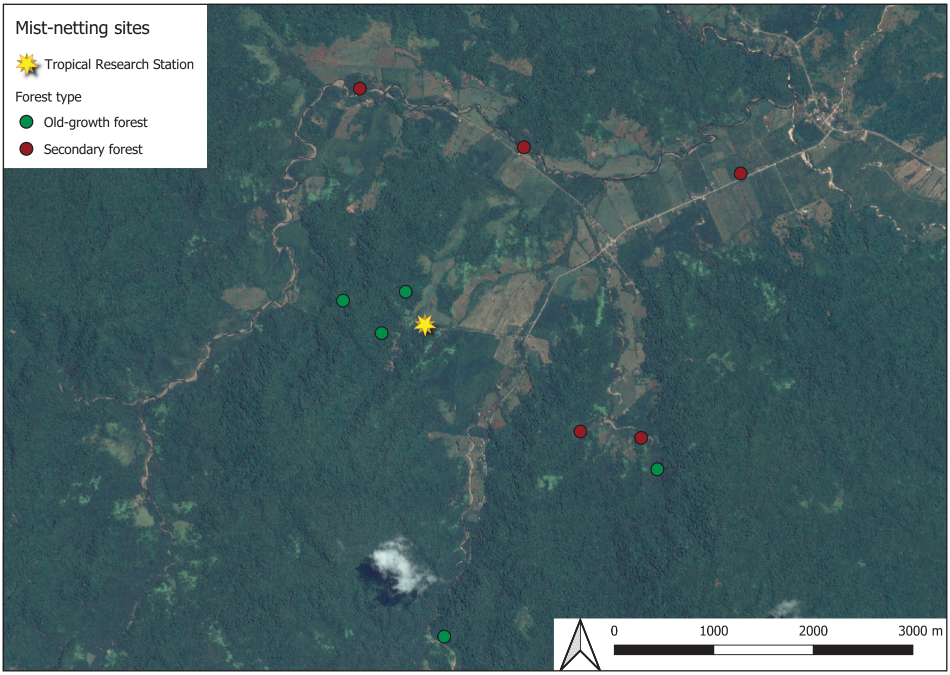

Fig. 1: Map indicating the mist-netting sites used to assess the composition of understory bird assemblages in young secondary forests and old-growth forests. – Abb. 1: Karte der Netzstandorte für die Untersuchung der Artenzusammensetzung von Unterwuchsvogelgemeinschaften in jungen Sekundärwäldern und alten Wäldern.

(± SD) was only 59.70 (± 0.67) and 59.75 (± 0.35) hours in old-growth and secondary forest, respectively. As the difference was extremely small, we assume that understory birds were sampled with an identical sampling effort in both forest types. As the focus was on diurnal understory forest birds, waterbirds (American Pygmy Kingfisher: 1 bird mist-netted) and nocturnal birds (Common Pauraque: 2 birds mist-netted) were excluded from all analyses.

Assessing bird assemblages across a gradient of vegetation succession

To study how forest bird assemblages change with progressing vegetation succession, birds were assessed using point counts at study sites representing a chronosequence of forest succession. Hence, five different habitat types were sampled, ranging from pastures with scattered shrubs and small trees, to planted young secondary forests, naturally regenerated young secondary forests, old cacao agroforestry systems and naturally regenerated old secondary forests (Fig. 2). Four replicate sites were selected per habitat type. Sites were located between N 08°41.112'– N 08°43.308' and W 083°11.828'–W 083°12.277' at altitudes between 67–146 m a.s.l. The size of each surveyed habitat patch was >1.5 ha with homogeneous vegetation and similar biotic characteristics among the habitat categories. The minimum distance between studied sites was 200 m, which is reported to make survey points statistically independent (Gutzwiller 1991, Whitman et al. 1998, Barlow et al. 2007a, 2007b, Edwards et al. 2011). All census points were located on private farm areas; some of these areas are part of a forest restoration project developed by the Tropical Research Station "La Gamba" in collaboration with the local community. Other sites were situated on abandoned land once used for agricultural purposes. All sites had a similar distance to areas of old-growth forest (<300 m to forest margin). A one-way ANOSIM testing for differences in spatial distances between census points belonging to the same habitat type did not indicate a significant effect, thus indicating that spatial autocorrelation should not weaken our results (Global $R = 0.005$, $p = 0.439$).

To assess the bird assemblages, point counts were conducted between 22 November 2010 and 27 January 2011. Each census point was visited ten times between dawn and 10:00 a.m., which should allow for recording of a large proportion of the sites' bird species (Ralph et al. 1995). Each point count lasted for 20 minutes. The order of surveyed census points was random to avoid a sampling bias that can be caused by a reduction in bird activity during the course of the day (Blake 1992, Blake & Loiselle 2001). Bird species were recorded visually and acoustically within a radius of 30 m. Unfamiliar bird songs, or songs from birds that could not be visually identified (Parker 1991), were recorded using a Telinga Pro7 StereoDat-Microphone and a Foster FR-2 recorder. Bird identifications were facilitated using Garrigues & Dean (2007). Recorded bird songs were then identified with the help of Isabell Riedl (University of Vienna), who had two years of experience with bird identification in this region. Additionally, the xeno-canto online-database (http://www.xeno-canto.org/), CD recordings by Ross Jr. & Whitney (1995), Ross Jr. (2000), and Boesman (2006) were used for identification.

Birds that were observed flying over the census-point, birds without obvious direct habitat affiliation (swifts, swallows), all freshwater birds (ducks, herons, kingfishers, waders etc.), birds with a nocturnal life mode (nightjars, owls) and those bird species associated with open land habitats were not considered in any statistical analysis (Borges & Stouffer 1999, Schulze & Riedl 2008). Birds were classified according to their habitat affinity as forest specialists (restricted to old-growth forest), forest generalist and open country bird species (Stiles & Skutch 1989, Schulze & Riedl 2008, Tebb 2008, Seaman & Schulze 2010). Nomenclature and taxonomy refer to Gill & Donsker (2012).

The vegetation structure of all study sites was characterized by measuring six variables within a radius of 30 m around census points: density of large trees, density of small trees, maximum tree height, canopy closure, understory density and herb cover. These variables have been shown to be important in similar studies (e.g. Thiollay 1999, Barlow et al. 2007b, Abrahamczyk et al. 2008, Reid et al. 2012). Large trees were defined as trees with a diameter at breast height (DBH) greater than 10 cm. Small trees were defined as trees with a height not larger than 10 m. These two measurements are important to quantify the structural diversity of woody vegetation in secondary forests (Guariguata et al. 1997, Guariguata & Ostertag 2001). Height of the tallest tree was measured with a range finder (Nikon Laser 1200S). To quantify canopy closure, a photograph of the canopy was taken directly above the census point. This was then digitalized and processed with a free software photo editor ImageJ 1.44p (Abramoff et al. 2004). The editing process involved changing the photos to binary mode in which pixels will have values for black/white colours. Then it is possible to analyze canopy closure in terms of percentage of pixels. Un-

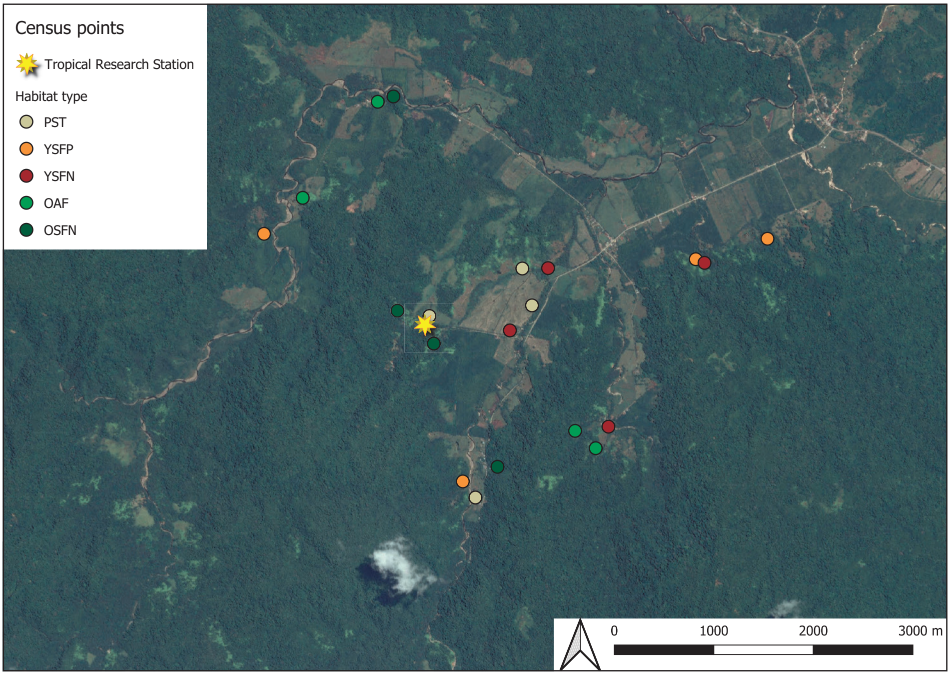

Fig. 2: Map indicating census points at which bird counts were conducted to assess bird assemblages in five different habitat types ranging from pastures with scattered shrubs and small trees (PST), to planted young secondary forests (YSFP), naturally regenerated young secondary forests (YSFN), old cacao agroforestry systems (OAF) and naturally regenerated old secondary forests (OSFN). – Abb. 2: Karte der Zählpunkte, an denen Vogelzählungen zur Ermittlung der Vogelgemeinschaften in fünf verschiedenen Habitattypen durchgeführt wurden: Weide mit vereinzelten Büschen und niedrigen Bäumen (PST), gepflanztem jungen Sekundärwald (YSFP), natürlich regeneriertem jungen Sekundärwald (YSFN), altem Kakao Agroforstsystem (OAF), und natürlich regeneriertem alten Sekundärwald (OSFN).

derstory density was determined by taking twenty different distance measurements to the nearest tree stem or bush around the census point above 1.5 m height. The twenty measurements were averaged into a single estimate value; this was done using a laser distance measurement device (Leica DISTO™ D2). Herb cover was estimated as percentage cover, taking into account all herbaceous species, and some low woody plants less than 15 cm tall.

Assessing temporal succession of birds at Finca Amable

To assess changes in species richness and composition of bird assemblages at the reforestation site Finca Amable, a total of seven bird surveys were conducted between July 2013 and November 2018. Every survey unit consisted of two zig-zag transects covering the entire area of the reforestation area (4 ha). The two surveys per unit were on average 13 days apart (min.-max. = 5–19 days). Average survey time was 204 min (max.-min = 182–243 min). During each survey unit, all acoustically and visually detected birds were counted, trying to avoid double counts.

Data analysis

Recorded species richness of bird assemblages recorded by mist-netting at the five old-growth and the five secondary forest sites was compared using a t-test. We further calculated species accumulation curves for both groups of forest sites using the iNEXT package (Hsieh et al. 2014). Similarity relationships of species assemblages assessed by mist-netting at the 10 forest sites were assessed using Bray-Curtis similarities (based on square-root transformed abundances, not considering recaptures). Subsequently, similarity relationships between sites were visualized using a non-metric multidimensional scaling (NMDS) ordination. The ordination was considered to reliably visualize similarity relationships when the associated *stress* value was <0.2 (Clarke 1993). A one-way ANOSIM was calculated to test for differences in species composition between the two forest types.

To identify relationships between the number of recorded species of forest generalist as well as forest specialist birds and the habitat variables, Pearson correlations were calculated. Afterwards, False Discovery Rate (FDR) transformations were applied to correct for bias caused by multiple testing (Pike 2011).

Changes in bird species composition between surveys over the time period 2013–2018 at the reforestation site Finca Amable were quantified using Bray-Curtis similarities (using square root transformed abundances) and visualized in a NMDS ordination. Since we expected species composition to change with progressing forest succession, extracted Dimension 1 and 2 values of the resulting NMDS ordination were correlated with the survey period order using a Spearman rank correlation. A Spearman rank correlation was also used to test if the total number of recorded bird species and in particular the relative richness of forest bird species changed with progressing forest succession.

Results

Species richness and species composition in old-growth and secondary forests

Species assemblages assessed by mist-netting were very similar in terms of species richness in both forest types, with a mean number of recorded species (± Std.dev.) of 31.6 (± 7.37) and 32 (± 7.81) species recorded per site in old-growth and secondary forest, respectively

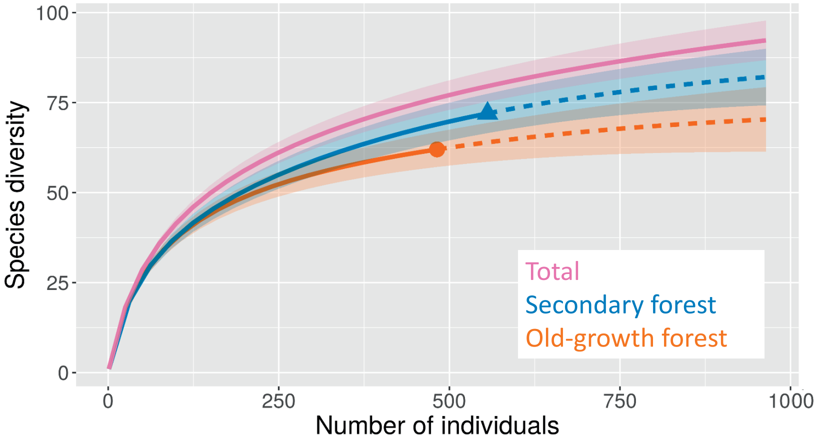

Fig. 3: Species accumulation curves with 95 % confidence intervals for the two forest types old-growth and secondary forest. Additionally, the curve for all sites combined is provided. – Abb. 3: Artenakkumulationskurven mit 95 % Konfidenzintervallen für alten Wald und Sekundärwald. Zusätzlich wird die Kurve für die Gesamtheit aller Standorte gezeigt.

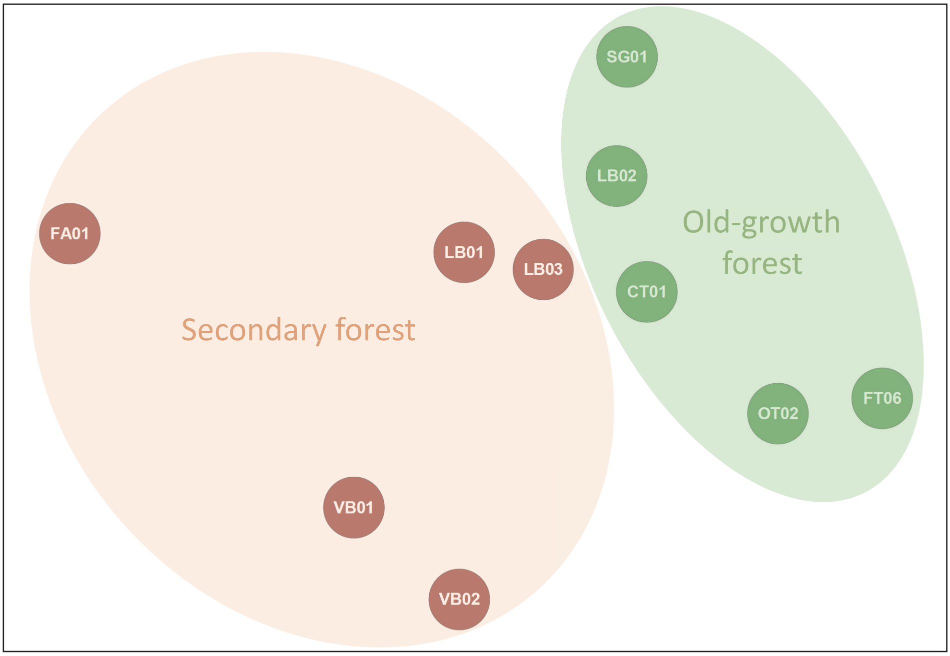

Fig. 4: NMDS ordination based on Bray-Curtis similarities (with square root transformed abundances) visualizing similarity relationships of understory bird assemblages assessed by mist-netting at five secondary and five old-growth forest sites. *Stress* = 0.04. – Abb. 4: NMDS-Ordination basierend auf Bray-Curtis-Ähnlichkeiten (mit wurzeltransformierten Abundanzen). Visualisiert werden die Ähnlichkeitsbeziehungen von Unterwuchsvogelartengemeinschaften, die an fünf Sekundärwaldstandorten und fünf Standorten in altem Wald mittels Japannetzfang untersucht wurden. *Stress* = 0,04.

(t-test: t = 0.08, p = 0.9357). Species accumulation curves calculated for both groups of forest sites did indicate a slightly lower richness of old-growth understory birds (Fig. 3). In contrast, species composition differed clearly between both forest types as indicated by the NMDS ordination (Fig. 4) and by a calculated one-way ANOSIM (Global R = 0.456, p = 0.008). However, two of the secondary forest sites (LB01 and LB03) were characterized by species assemblages which closely resembled old-growth forest ones (Fig. 4).

Of the 95 mist-netted understory bird species, 42.5 % were recorded in both forest types, while 23.4 % and 34.0 % of the species were unique to old-growth and secondary forest, respectively. When excluding species which were only mist-netted once or twice as they

Tab. 1: Results of Pearson correlations between habitat variables and species richness of forest specialists and forest generalists. Results printed in bold remained significant after calculating the False Discovery Rate. – Tab. 1: Ergebnisse von Pearson-Korrelationen zwischen Habitatvariablen und Artenreichtum von Waldvogelspezialisten und -generalisten. Fettgedruckte Ergebnisse waren auch nach Berechnung der Falscherkennungsrate signifikant.

Habitat variables	**Forest specialists**		**Forest generalists**	
	R	**FDR-adjusted *p***	***R***	**FDR-adjusted *p***
Herb cover	-0.55	**0.023**	-0.01	0.953
Maximal tree height	0.60	**0.014**	0.51	**0.038**
Large trees	0.85	**<0.001**	-0.02	0.953
Understory density	-0.61	**0.014**	-0.09	0.787
Small trees	0.37	0.143	0.50	**0.038**
Canopy closure	0.59	**0.014**	0.30	0.252

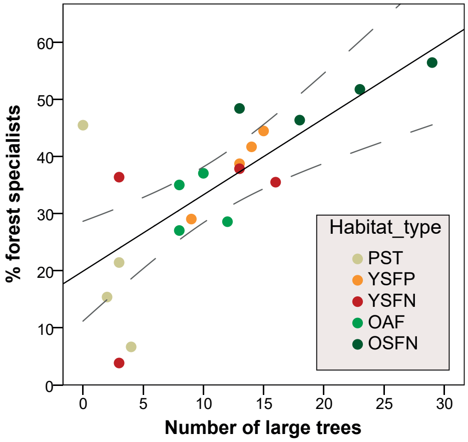

Fig. 5: Relationships between percentage of forest specialists at census points and the number of large trees. Different symbol colours indicate the habitat types: PST – Pastures with scattered shrubs and small trees, YSFP – planted young secondary forests, YSFN – naturally regenerated young secondary forests, OAF – old agroforestry systems and OSFN – naturally regenerated old secondary forests. – Abb. 5: Zusammenhang zwischen Anteil an spezialisierten Waldvögeln an den Zählpunkten und der Zahl großer Bäume. Die Symbolfarben zeigen unterschiedliche Habitattypen: PST – Weide mit vereinzelten Büschen und niedrigen Bäumen, YSFP – gepflanztem jungen Sekundärwald, YSFN – natürlich regeneriertem jungen Sekundärwald, OAF – altem Agroforstsystem, und OSFN – natürlich regeneriertem alten Sekundärwald.

are very rare or difficult to trap, figures change substantially. Of the remaining species, as many as 66.1 % could be recorded in both forest types, while only 15.3 % were unique to old-growth forest and 18.5 % were only mist-netted in secondary forest.

Species richness and species composition across a chronosequence of vegetational succession

A total of 115 forest bird species were recorded during the point counts, including 61 species classified as forest generalists and 54 classified as forest specialists. Richness of forest specialists was most strongly related to the number of large trees in that the number of specialist species increased significantly with the increasing number of large trees. Other variables were only weakly (herb cover, maximum tree height, canopy closure, understory density) or not significantly related to the richness of forest specialists. Variance in species numbers of forest generalists was only weakly positively related to the maximum tree height and the density of small trees (Tab. 1). While the total number of bird species recorded at census points was not related to the number of large trees ($r = 0.036$, $p = 0.8793$), the percentage of forest specialists increased significantly ($r = 0.702$, $p = 0.0006$; Fig. 5).

Colonization of a reforested area by forest birds

Bird species composition of Finca Amable changed almost continuously with progressing forest succession as Dimension 1 values of the resulting NMDS ordination (Fig. 6) are correlated with the survey period order ($r_s = 0.942$, $p = 0.0028$). This change in species composition can be attributed to an increase of the relative richness of forest birds ($r_s = 0.893$,

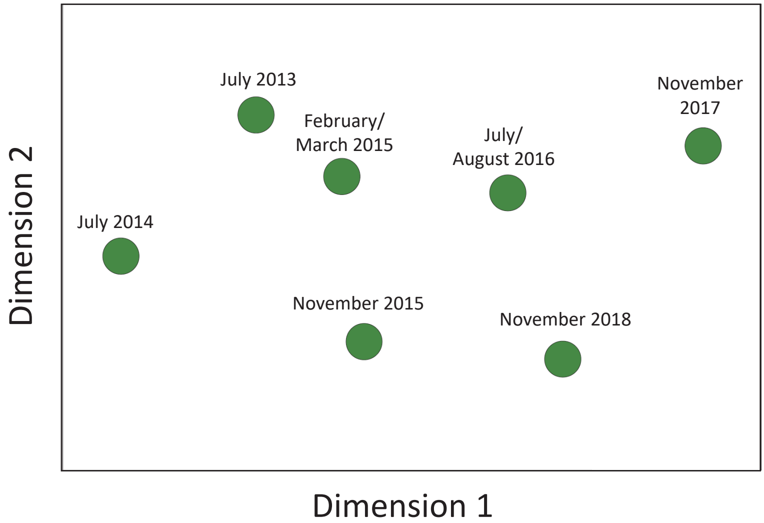

Fig. 6: NMDS ordination based on Bray-Curtis similarities (with square root transformed abundances) visualizing similarity relationships of understory bird assemblages surveyed at the reforestation area Finca Amable over a period of six years after the planting of the first trees. Stress = 0.01. – Abb. 6: NMDS-Ordination basierend auf Bray-Curtis-Ähnlichkeiten (mit wurzeltransformierten Abundanzen). Visualisiert werden die Ähnlichkeitsbeziehungen von Unterwuchsvogelartengemeinschaften, die auf der Wiederbewaldungsfläche Finca Amable über einen Zeitraum von sechs Jahren nach Beginn der Baumpflanzungen untersucht wurden. Stress = 0,01.

p = 0.007; Fig. 7), while the total number of recorded species per survey did not change within the period of five years (r_s = 0.206, p = 0.658).

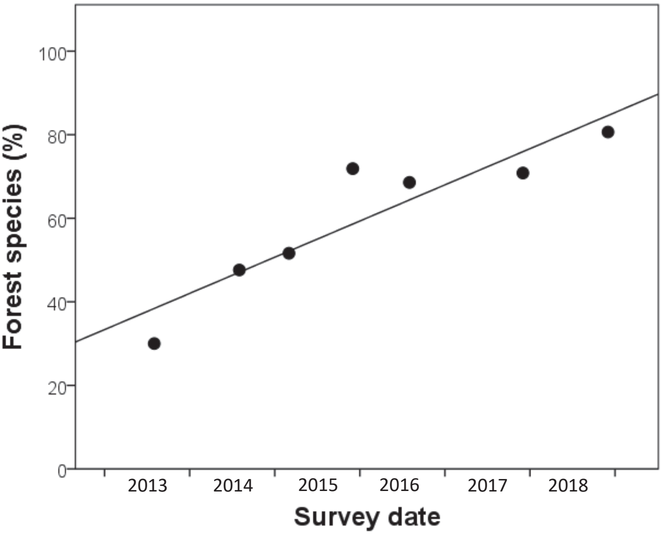

Fig. 7: Change in the relative richness of forest bird species surveys at the reforestation area Finca Amable over a period of six years after the planting of the first trees. – Abb. 7: Veränderung der relativen Artenvielfalt von Waldvogelarten am Wiederbewaldungsstandort Finca Amable über einen Zeitraum von sechs Jahren nach Beginn der Baumpflanzungen.

Discussion

The importance of secondary forest for forest birds

Although understory species assemblages assessed by mist-netting at old-growth forest and young secondary forest sites showed a similar species richness, both forest types differed clearly in species composition. However, a substantial proportion of old-growth forest species could also be found in young secondary forest. It must also be emphasized that, in the latter forest type, several forest species were also recorded which appear to prefer disturbed forest, underlining that such secondary forest patches also contribute to the local forest species richness. For example, the 21 individuals of Cherrie's Tanager (*Ramphocelus costaricensis*), an endemic of the Pacific slope of Costa Rica and Panama, were all mist-netted in young secondary forests. Other common (>8 trapped individuals) resident breeding birds exclusively trapped in secondary forests were Buff-throated Saltator (*Saltator maximus*) with 10 individuals, Clay-colored Thrush (*Turdus grayi*) with 22 individuals, Northern Royal Flycatcher (*Onychorhynchus mexicanus*) with 9 individuals, Stripe-throated Hermit (*Phaethornis striigularis*) with 10 individuals and White-tipped Dove (*Leptotila verreauxi*) with 18 individuals. Only two of the more common resident birds were exclusively trapped in old-growth forest, the Rufous Mourner (*Rhytipterna holerythra*) with 11 individuals and the Sulphur-rumped Flycatcher (*Myiobius sulphureipygius*) with 12 individuals. Our results also underline the importance of secondary forest for northern migrants, as all of the 15 individuals of the Northern Waterthrush (*Parkesia noveboracensis*) were mist-netted in young secondary forests. The importance of secondary forest for northern migrants was already reported by other studies from the Neotropics (Karr 1976, Martin 1985, Reid et al. 2008). It was even assumed that several of the Nearctic migrants can play an important role as seed dispersers and, hence, contribute substantially to the regeneration of young secondary forests (Blake & Loiselle 1992, Reid et al. 2008).

Secondary forests predominantly support generalists (Brook et al. 2003) and probably act as reproductive "sinks" for some forest species (Battin 2004, Peh et al. 2005, Aubrecht & Schulze 2008). However, the total of 115 species of forest-depending birds (with 47 % classified as forest specialists) recorded in secondary forests of our study area by point counts underlines their substantial contribution to bird diversity on the landscape level. That secondary forest may result in an increase of species richness at a regional level was already emphasized by other studies (Graham & Blake 2001, Hughes et al. 2002).

Furthermore, the conservation value of secondary forest sites is highlighted by our records of several range-restricted forest species such as the Charming Hummingbird (*Amazilia decora)*, Baird's Trogon (*Trogon bairdii*), Black-hooded Antshrike (*Thamnophilus bridgesi*), Riverside Wren (*Cantorchilus semibadius*), Black-cheeked Ant-Tanager (*Habia atrimaxillaris*) and Spot-crowned Euphonia (*Euphonia imitans*), and the near threatened forest specialist species, the Golden-winged Warbler (*Vermivora chrysoptera*).

Large trees as key habitat structure for forest birds

Across our census point sites representing a gradient of vegetational complexity, large trees emerged as an important variable for the richness of forest-dependent species. Overstory tree density also proved to be an important explanatory variable for differences in the species richness of various functional groups of forest birds across a gradient from natural forest to secondary forest, agroforestry systems and annual cultures in Cameroon (Waltert et al. 2005). Some earlier studies highlighted canopy closure and structural complexity (i.e. number of vegetation layers) of secondary vegetation as important determinants for the species richness and the composition of tropical forest birds (Blake & Loiselle 2001, George & Zack 2001, Dunn 2004, Barlow 2007b, Borges 2007). The number of large trees contributing to the vertical complexity of secondary forests and the canopy closure seemed to influence the species richness of specialist birds also at our study sites. However, the effect of the number of large trees appeared to have a particularly important role for the occurrence of forest specialist bird species (but not forest generalists). The value of large trees as a key structural element for many forest birds, providing breeding niches and food resources, has already been emphasized by other studies (Sodhi et al. 2005, Van Bael et al. 2007, Abrahamczyk et al. 2008). However, the presence of large trees may only facilitate the colonization of young secondary forests by bird species that require living trees, because such young forests are mostly still lacking larger dead trees (Dewalt et al. 2003).

Although early stages of forest succession may not be appropriate breeding habitat for many forest specialists (MacArthur & MacArthur 1961, Bowen et al. 2007), at least some of them may infrequently use various resources provided by this forest type, e.g. when situated close to the margin of old-growth forest. For example, at one of our pastures with scattered shrubs and small trees, eight forest specialist species were reported. Most of these being omnivorous (i.e. *Attila spadiceus*, *Cyanocompsa cyanoides*, *Euphonia imitans*, *Ornithion semiflavum* and *Ramphastos swainsonii*), but also including one insectivore (*Pachyramphus aglaiae*), one granivorous (*Leptotila cassini*) and one frugivore species (*Penelope purpurascens*). The presence of such forest specialist bird species can be explained by the presence of single larger remnant trees (Guevara et al. 1986). Such scattered large trees are considered to be keystone structures in human-modified areas, offering benefits to forest birds, not only at a landscape level (e.g. connectivity) but also locally (e.g. structural complexity, nesting) (Manning et al. 2006).

Importance of secondary habitats as corridors for the conservation of forest birds

The relatively high number of forest-dependent species recorded in secondary forests indicate that they may also have a high potential to improve connectivity between remaining areas of old-growth forests in our study area. In fact, even smaller groups of trees embedded in the human-dominated landscape can already be utilized by at least some forest birds as stepping stones for dispersal movements between forest fragments (Gillies and Cassady St. Clair 2010). In contrary to the assumption that the majority of tropical forest birds have a very limited dispersal capability, a recent study from southeastern Brazil reported movements of forest birds between forest fragments across open areas of up to 650 m (Marini 2010). Although direct evidence (e.g. by recaptures of banded birds) is still missing, we can thus expect that most of the secondary patches in our study area can act as stepping stones for at least a certain proportion of forest birds, as the majority of them is located well within a distance of less than 500 m to the margin of larger forest areas. Besides their importance as stepping stones, secondary forests attached or adjacent to mature forest may increase the habitat quality for forest species in the buffer zone around mature forest, thus reducing negative edge effects (Fischer et al. 2006).

Rapid colonization of secondary forest patches by forest birds

A recent meta-analysis documented that species richness of different vertebrate groups, including birds, reached a level in secondary forests similar to that of mature reference forest sites within a couple of decades of natural succession. However, species compositional similarity still differed even between old secondary forests and mature or old growth forest. In birds, the main reason may be the delayed recovery of forest specialists and functional groups such as insectivorous birds (Acevedo-Charry & Aide 2019). This is also emphasized by our study on the recovery of forest species at the reforestation site Finca Amable. Although the relative contribution of forest species, including forest generalists able to utilize disturbed forests, dramatically increased from 30 to nearly 80 % during a period of only six years after the start of the reforestation, true forest specialists common in adjacent mature forest (e.g. Black-cheeked Ant-Tanager) are still missing. Another study on birds comparing data from 44 tropical secondary forest patches with nearby primary forest sites also indicated that the species richness of forest specialists increased continuously with secondary succession but reached similar species richness of forest specialists only after 100 years (Sayer et al. 2017).

Conclusions

Besides potentially representing important stepping stones for forest birds by facilitating crossings of open areas, our results indicate that secondary forest patches embedded with the human-modified landscape can represent important secondary habitats for a substantial proportion of forest birds. Additionally, when attached to the forest margin they may act as important buffer habitats at the border of protected forest areas. Hence, conservation efforts should aim to protect such emerging forest structures and additionally should target to increase the density of such forest patches to enhance the permeability of the human-modified landscape. Such measures will not only contribute to interconnecting remaining fragments of old-growth lowland rainforest but will improve the function of the biological corridor COBIGA as a link between the lowland forest zone and the adjacent mountain range further inland (Weissenhofer et al. 2008b). This may also help to maintain and perhaps partly re-establish elevational movements of forest birds between forests of the adjacent mountain range and the larger lowland forest blocks (e.g. Piedras Blancas National Park).

Although secondary forests cannot replace old-growth and undisturbed forest (Sayer et al. 2017, Acevedo-Charry & Aide 2019), they represent an important landscape structure contributing to maintaining biodiversity. This is particularly important as biodiversity is declining even in protected areas (Laurance et al. 2012). Consequently, young secondary forest should be protected, particularly in human-dominated landscapes where only small patches of mature forest remain (Sayer et al. 2017).

Reforested and naturally regenerating young forests proved to be of similar importance for forest birds. However, considering the close relationship between the number of large trees and the richness of forest specialists, further research has to evaluate the potential of using fast-growing trees to more rapidly increase the conservation value of actively restored secondary forests for the recovery of forest birds, particularly forest specialists. Potential candidate trees could be fast-growing native species such as *Terminalia amazonia* (Combretaceae) and *Vitex cooperi* (Verbenaceae) (Lechner et al. 2012).

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